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STUDIES OF THE RECENT BREEDING SUCCESS OF THE PEREGRINE, *FALCO PEREGRINUS*

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Summary. Between 1956 and 1963, the breeding population of peregrines in Great Britain suffered a severe decline, especially in southern parts, to about half its former numbers. This 'crash' was preceded, from 1947 onwards, by a widespread decrease in eggshell thickness, and later by an increase in parental egg-breaking. During 1956 to 1963, many pairs which laid eggs failed in their nesting, and many others did not lay eggs at all, so that breeding success of the remaining population was low. Decline in numbers and in breeding success are attributed mainly to contamination of the peregrine population by persistent, toxic organochlorine residues. The various symptoms of reduced reproductive success, and their possible interrelationships, are discussed, together with the respective contributions of direct mortality factors and reproductive failure to decline and subsequent status of the peregrine population.

The problem

In the late 1950s, ornithologists became aware that one of the most cherished species of the British avifauna, the peregrine, *Falco peregrinus*, showed a rapid decline in numbers and output of young after a long period distinguished in most districts by a remarkable stability of breeding population. From the viewpoint of nature conservation, the problem was threefold; to assess the scale and rate of the decline over Britain as a whole, to determine the causes of decline and, if possible, to reverse the trend. The problem as a whole thus involved a study in applied ecology, but the examination and analysis of the field situation has illuminated points of approach in more fundamental and experimental studies aimed at understanding causation in depth.

Breeding success

The criterion of breeding success adopted here is total output of fledged young as a proportion of total population. There are different elements within this overall relationship, any one of which can be limiting, and therefore regarded as a measure of breeding success in itself.

1. Proportion of the population paired and holding breeding territory/cliff.
2. Proportion of the population laying eggs, average clutch size and total ber of eggs laid.

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3. Proportion of eggs and clutches hatched, average number of chicks per clutch, and total number of chicks hatched.

4. Proportion of pairs (in category 1 or 2) rearing young, average number of young per fledged brood, and total number of fledged young.

The historical picture

The reduction in the number of peregrine falcons in Britain since 1956 has been paralleled by a decline, sometimes even more severe, in the populations in various parts of northern and northwestern Europe and North America (Hickey, 1969). In Britain, there has been some reduction in nearly all the main elements which contribute to breeding success. In considering the 'normal' peregrine situation here it is necessary to go back to the pre-1940 period because peregrines in southern England were almost exterminated during 1940 to 1945, and numbers were reduced in some other districts, though there was considerable yet not complete recovery between 1945 and 1955.

It is estimated that, on average, about 700 pairs of peregrines annually attempted to breed in Great Britain during 1930 to 1939. Information on their breeding biology is somewhat haphazard and incomplete, but the great majority of territory-holding pairs actually laid, and most of the pre-laying failures were through gamekeeper destruction of birds or pairs. A fairly high proportion of pairs which laid in England and Wales failed totally in their breeding every year through the relentless robbing of first and repeat clutches by egg collectors. On the grouse moors of the north, especially eastern Scotland, many females were also shot off eggs or trapped every year. This persecution apparently had no effect on the number of pairs annually attempting to nest during 1930 to 1939 (nor for a much longer period), and the population was evidently maintained by a high output of young from remoter districts of northwestern Scotland and Ireland. It is not known to what extent the British population was boosted by peregrines from continental Europe, or vice versa, but it is possible that there was some replenishment from this source.

Mean clutch size was about 3·5 eggs, and mean number of fledged young per brood was 2·5. The losses between laying and fledging were probably divided about evenly between hatching failures (chiefly addled eggs) and nestling mortality. Probably a majority of eyries in which eggs hatched succeeded in producing at least one fledged young, and most of the failures at this stage were the result of keeper activity, with only a small proportion of broods destroyed by pigeon fanciers or removed by falconers.

Most of the considerable breeding failures during the period 1930 to 1939 thus resulted directly from adverse human activity. The remarkable feature is that, despite these considerable annual depredations, the breeding population remained almost constant in each successive year, even in districts where only a handful of young were reared each breeding season. There is, indeed, a good deal of circumstantial evidence to show that there was in these years a substantial non-breeding surplus of peregrines which rapidly filled any gaps in the breeding population during the current or following breeding season. Numerous instances of rapid re-mating of one survivor of a pair have been quoted, especially by keepers, and an example was known in 1971 (D. N. Weir, personal communi-

cation); some nesting places, in fact, seem to have had a quite alarming capacity to drain off a succession of peregrines each year, as each newcomer or pair was eliminated by the zealous keeper.

Nevertheless, it would seem that, before 1939, the peregrine breeding population was limited not by lack of recruits, but by availability of suitable nesting places (cliffs or remote rocky islands) and by the territorial demands of the species. Almost all suitable cliffs were occupied up to the point where territory kept adjacent pairs spaced out. This spacing was markedly regular, but varied in actual magnitude and the variations seemed to be obviously related to differences in food supply, being closest (about 1·6 miles or less) in southern England and certain northern sea-bird colonies, and farthest apart (6 miles or more) in the barren interior of the northern Highlands. Over much of Britain, the average distance between contiguous pairs was about 3 miles. It is likely that for the non-breeding surplus which was not drawn upon in compensating for losses amongst territory-holding peregrines, there existed a rapid mortality gradient as attempts were made to colonize marginal habitats—as occurs in the red grouse, *Lagopus lagopus* (Jenkins, Watson & Miller, 1963).

It is evident that, in districts not affected by war-time 'control', much the same situation persisted in the peregrine population up to 1955, in that stability of numbers and regular spacing of occupied eyries were a highly characteristic feature of most areas where cliffs were plentiful, and indicated 'saturation' breeding density. There was, however, one new feature—that from about 1951 onwards many eyries failed to produce young because the eggs were broken and probably eaten by the parent peregrines themselves, or disappeared in circumstances which suggested that the parents were responsible. Then, after 1955, other changes became apparent—many territories in England and Wales, once regularly occupied, became deserted, and many of those remaining occupied were held by single birds or non-breeding pairs. Clutch depletion was frequent among pairs still producing eggs, and the total output of young became reduced even in remote districts. This 'decline syndrome' spread northwards and by 1962, when a national survey was made, only inland districts of the central and eastern Highlands seemed to be relatively free of these symptoms of population ill-health (Ratcliffe, 1963). Population decline continued into 1963 but then seemed to level off at about 44% of the numbers before 1939, and after 1966 there has been a slow but appreciable recovery in inland northern districts (north of Wales), but virtually no change in most northern coastal districts, or in any part of Wales or southern England, where, respectively, only 22% and 13% of pre-war populations remained in 1971 (see Tables 1 and 2).

Mechanisms involved in reduced breeding success

Reduction in breeding success was regarded as part of a general syndrome of decline, with population 'crash' as its final and extreme expression. The actual decline in numbers was interpreted as the fairly direct effects of persistent organochlorine insecticides in causing increased adult mortality. The pattern of decrease, both geographically and in time, showed a close correlation with the introduction and subsequent widespread use of the highly toxic cyclodiene insecticides (dieldrin, aldrin and heptachlor) as seed dressings. Various raptors

Table 1. Status of peregrine population and breeding success in 1962 and 1971

	1962					1971				
(1)	(2)	(3)		(4)		(5)	(6)		(7)	
Region	*Expected population in territories visited*	*No. of territories with peregrines present*		*No. of broods seen*		*Expected population in territories visited*	*No. of territories with peregrines present*		*No. of broods seen*	
		No.	*% of* 2	*No.*	*% of* 2		*No.*	*% of* 5	*No.*	*% of* 5
Southern England	60	5	8	2	3	76	10	13	5	7
Wales	75	19	25	3	4	118	26	22	5	4
Northern England	45	22	49	3	7	55	31	56	13	24
Southern Scotland	38	23	61	2	5	50	38	76	12	24
South and East Highlands	84	65	77	39	46	153	126	82	71	46
North and West Highlands	130	107	82	43	33	177	110	62	51	29
Total for Great Britain	432	241	56	92	21	629	341	54	157	25

In 1962, 60% of known breeding territories were examined; in 1971, 90% were examined. In 1962, nine broods (out of the ninety-one) were known to have been taken by falconers; in 1971, at least six broods were taken or destroyed. Figures in columns (4) and (7) thus do not give final breeding success, but indicate success up to the nestling stage. Expected population is that estimated for these territories for the 'normal' period 1930–1939.

Table 2. Status of peregrine population and breeding success in coastal and inland territories in 1962 and 1971

Region	*Coastal*				*Inland*			
	1962		1971		1962		1971	
	% *occupation*	% *broods*	% *occupation*	% *broods*	% *occupation*	% *broods*	% *occupation*	% *broods*
Southern England	8	3	13	7	0	0	0	0
Wales	18	0	20	3	31	5	25	5
Northern England	43	14	13	0	52	3	74	33
Southern Scotland	20	7	45	10	87	4	97	33
South and East Highlands	76	47	63	33	77	45	90	51
North and West Highlands	84	40	52	22	78	19	87	46
Total for Great Britain	48	21	36	14	65	21	75	37

Percentages are based on estimates of 'normal' population for the territories visited, i.e. the numbers which could have been expected during 1930 to 1939 Nearly all peregrine territories in southern England are coastal, so that the south to north gradient of decline gave an initial bias against occupation of coastal territories.

and carnivorous mammals were exposed to secondary poisoning by feeding on seed-eating birds which had absorbed varying amounts of these chemicals; body loads of residues (especially of dieldrin, heptachlor epoxide and DDE) in peregrines found dead were considered to reach lethal levels for the species (Jefferies & Prestt, 1966).

The possible mechanisms were obscure until it was discovered that decrease in eggshell thickness appeared to be closely involved. This change has been shown in eggshells of the peregrine (19·1% nationally); sparrow hawk, *Accipiter nisus* (17·2%); merlin, *Falco columbarius* (12·7%); golden eagle, *Aquila chrysaetos* (9·9%); kestrel, *Falco tinnunculus* (4·9%); hobby, *F. subbuteo* (5·2%); shag, *Phalacrocorax aristotelis* (12·3%); rook, *Corvus frugilegus* (5%); and carrion crow, *C. corone* (4·8%) in Britain (Ratcliffe, 1970). Similar changes are known to have occurred in the peregrine and other raptors in North America (Hickey & Anderson, 1968) and in various continental European raptorial and fish-eating birds studied by Hickey & Anderson and by J. H. Koeman (personal communications). In the peregrine and sparrow hawk, the onset of the eggshell change has been accurately dated to 1946–47, when DDT and gamma-BHC were first introduced. The effect in the population was sudden and reached a plateau by 1950. Decrease in shell thickness has obvious implications for increase in egg breakage, and it is a reasonable assumption that the two phenomena are closely connected.

It has been firmly established that organochlorine residues (DDE, dieldrin and PCBs) at field levels of contamination, can cause decrease in eggshell thickness (see Jefferies, 1973). Blus, Gish, Belisle & Prouty (1972) have shown that eggshell thickness decreases as DDE concentration increases, but that the relative effect is greatest at the lower residue levels and falls off as these rise; this concentration-effect relationship follows a similar pattern in different species, but evidently operates at different levels in different species.

This is an example of a completely unexpected accidental side effect of a chemical pollutant on a non-target species. The eggshell phenomenon occurs on a wide, perhaps global, scale. In all districts of Britain, eggs of the peregrine examined after 1947 have had shells significantly thinner than the median for pre-1947 eggs; only in the central and eastern Highlands does the difference fail to reach a high level of significance ($P < 0{\cdot}001$). Moreover, the eggshell effect (as distinct from eggbreak) was not detected until 20 years after its onset.

As the mean shell thickness becomes progressively reduced the likelihood of mechanical damage increases. This stage certainly seems to have been reached in the Californian population of the brown pelican, *Pelecanus occidentalis* (Risebrough, Sibley & Kirven, 1971), in which some birds have laid soft-shelled eggs. It is less certain that such a direct cause-effect relationship holds at lower levels of shell-thinning. Milstein, Prestt & Bell (1970) and I. Prestt (unpublished) have some interesting data for the heron, *Ardea cinerea*, in Britain: one colony produced eggs with a mean reduction in shell thickness (compared with pre-1947 specimens) of 20%, yet at the end of the breeding season about 70% of pairs had succeeded in producing at least one young. There was much egg-break as the result of which the birds laid up to three clutches. Egg losses

decreased as the season went on, so that, by the end, most pairs hatched one clutch. It was observed directly (from a pylon hide) that at least some eggs were broken by birds suddenly stabbing them and flicking them out of the nest, as though performing nest-cleaning actions.

The implications are that, in the British peregrine, which has also suffered a 19% decrease in eggshell thickness, some of the breakages may be behavioural and occur without prior mechanical damage as a stimulus. Some of the thinnest shelled peregrine eggs are probably prone to mechanical damage in the nest, and a few dented eggs have been seen in recent years. Nevertheless, a great many relatively thin-shelled peregrine eggs undoubtedly hatch annually, and the difference, compared with the heron, seems to be that peregrines produce fewer 'repeat' clutches and tend to destroy those which they manage to lay.

It is possible, therefore, that eggbreaking in the British peregrine is mainly a behavioural, rather than mechanical effect. This view is supported by certain field observations. Some individual peregrines are habitual egg breakers, whereas in the same area others which lay equally thin-shelled eggs are not. Peregrines which have broken their eggs often continue to brood on the empty nest, sometimes with the shell remains in it. Three cases have been known in which peregrines that had lost their own eggs then dispossessed kestrels of their clutches and incubated these; one of these peregrines hatched and successfully reared a brood of four kestrels. The female of this pair in another year was seen to indulge in nest-scraping (behaviour which usually precedes laying) when she had eggs, and actually kicked an egg out of the nest (G. Carse, personal communication).

Such behaviour would seem to suggest that organochlorine residues cause a biochemical disturbance which upsets normal behaviour patterns, and produces inappropriate reactions. Jefferies & French (1971) have shown the effects of these residues on the avian thyroid, and their possible implication in the behavioural responses. Could it be, for instance, that hypothyroidism in the peregrine causes a general recession of breeding activity, so that birds tend to behave, if only at times, in ways which would be inappropriate to the breeding season, This could explain such effects as disturbed incubation pattern, non-laying of eggs altogether, and the holding of nesting cliffs by apparently unpaired birds (the pair-bond in peregrines appears to weaken during the winter, for the sexes frequently separate and roost in different cliffs). Such effects as these might occur without overt changes in the reproductive organs. The biochemical and physiological mechanisms concerned in these aspects of reproductive failure might thus be different from those involved in eggshell thinning as such. Other mechanisms could clearly be involved in the apparent increase in frequency of addled eggs, and in the greatly increased incidence of non-breeding among territory holding pairs, and the review of Jefferies (1973) indicates some of the possibilities. The holding of territories by single birds, when following immediately after occupation by a pair, could simply be the result of death of the partner, combined with failure of the survivor to re-mate.

Whatever the exact nature of the mechanisms involved, it seems clear that the residues of persistent organochlorine compounds in the peregrine cause fundamental biochemical changes which are expressed in various parts of the whole reproductive process. The degree of change appears to be related to that of

contamination, and at the higher levels of contamination the net effect ranges from substantial impairment of reproduction to total failure; there is, however, a range of sensitivity in response at the individual level, and it is the expression of reproductive failure at the population level which is the crucial ecological feature.

Effect on population dynamics

Eggbreaking, whether directly related to eggshell thinning or not, has reduced the number of young produced through causing total or partial depletion of clutches. Many peregrines have only one or two eggs late in incubation when normal clutches of three or four have been seen earlier. Out of 208 clutches seen between 1951 and 1966, eighty-one (39%) were depleted by at least one egg after laying (Ratcliffe, 1970). In the central and eastern Highlands, mean brood size during 1961 to 1971 (2·44 young) remained close to the national pre-war figure (2·5), but elsewhere it is now often below 2·0 young and, in some districts, e.g. southern Scotland, it has remained consistently at about 1·9 young. Broods of only one young are now much more common than before 1947.

However, the important factor is whether the total reduction in output of young has any effect on maintenance of population. Although eggshell thinning began in 1946 to 1947 and eggbreaking was certainly frequent from 1951 onwards, the actual numbers of peregrines continued to increase up to 1955 in those districts which had been temporarily depleted by war-time 'control'. It is, moreover, evident that in areas such as the Lake District a pesticidal effect on breeding merely replaced an egg-collecting effect; in fact, in Lakeland, breeding success has probably been as high if not higher during each of the last 3 years than during any year between 1900 and 1947, when eggshell thinning began.

It is probable that the post-1955 'crash' in numbers resulted primarily from greatly increased adult mortality, which varied in the different areas; and that the stabilization occurring after 1963 reflected a halt in the further spread of this high mortality.

Table 1 indicates the geographical variations in territory occupation and number of broods of the peregrine in Britain during 1962 and 1971. In 1971, a few broods were known to be taken or destroyed, but it is believed that most of the 157 fledged successfully (105 were actually seen on the wing), so that these figures provide a reasonably good index of breeding success. Successful broods averaged 2·1 young, so that around 300 young peregrines were reared in 1971. Allowing for apparently unpaired birds, the known total of territory-holding adults or sub-adults during the same breeding season was 605. The average breeding success was thus about one young bird to every two adults or sub-adults. In terms of the existing population, this figure is not high, and in terms of the original population (700 pairs) it is extremely low.

Sample census data for the period of recovery since 1963 make it appear unlikely that the average net increase in occupied territories between successive years has exceeded ten. A similar projection can be extended to 1971–72. It is thus improbable that more than twenty of about 300 young from 1971 will go towards the net increase in the territory-holding population in 1972. Of the remaining

280 birds, some will fill gaps caused by losses in the 1971 territory-holding population; some may emigrate to continental Europe; some may continue to live in Britain, forming a non-breeding population not holding territories on nesting cliffs; and the remainder will die. The proportions involved in the last four possibilities are unknown. Mead (1969) found that of twenty peregrines recovered from 214 birds ringed in Britain, none had travelled beyond the British Isles, though eight birds ringed in Scandinavia were recovered in Britain. Undoubtedly, a certain number of territory holders (in at least five territories in 1971) on grouse moors are destroyed every year and, as suggested above, some of these keeper activities may drain the population to an unsuspected degree. Moreover, at least six adult peregrines were found dead or dying from other causes in 1971. However, since 1961, observations of individuals identifiable by their idiosyncracies of behaviour, voice and egg type suggest that there is not a rapid general turnover of the laying females, and that the average life-span of such birds in northern England and southern Scotland is no less than before the 'crash'.

Records of single peregrines in non-breeding areas, mainly lowland or coastal, have increased again during the second half of the 1960s, after reaching a low level in the earlier half. Most birds, including immature ones, were seen between August and March, and the smallest numbers of non-breeders during the breeding season were recorded from April to June. The appearance of birds in August and September corresponds to the time of dispersal of the young, and may also reflect a partial migration of adults from remote northern and western districts of Scotland, especially coastal areas, where the food supply becomes poor in winter. Some of these peregrines appear to winter in various parts of southern England and by the following April their numbers have declined. There is certainly no corresponding order of increase in the number of occupied territories in the breeding areas nearest to these wintering haunts. There is, thus, no clear indication of a substantial surplus of potential breeders forming a floating population during the spring.

The output of young from northern eyries seems adequate annually to provide a surplus of recruits which could re-occupy vacant territories at a rate capable of producing a steady recovery of the national population towards the pre-1939 level; there is evidence of an autumn and winter surplus in districts close to depleted areas, but recovery in occupation of deserted territories south of Yorkshire nevertheless still continues to be absent or negligible, and has been slow in all districts. There appear to be at least four possible reasons for this failure. Firstly, the actual size of the non-breeding surplus may be inadequate to generate sufficient 'pressure', especially if there is a marked tendency of individuals to return to the vicinity of their birthplace in order to breed. Secondly, despite an adequate surplus of new birds in winter, for some reason, perhaps connected with loss in continuity of occupation, the vacant territories fail to attract them. Thirdly, the output of young birds in any one year is largely absorbed in filling new gaps in the existing territory-holding population, so that the potential surplus has virtually disappeared by the following breeding season. Fourthly, an adequate surplus of new birds is available and would re-occupy vacant territories fairly rapidly, but is steadily extinguished by a heavy mortality as the breeding season approaches. A further possibility, related to the second

of those just outlined, is that a majority of birds fail to come into breeding condition.

Further problems emerge when the situation is examined on a more local scale. Recovery of population and breeding success in the Lake District has been pronounced since 1966 yet, despite an annual output of twenty to thirty young during each of the last three breeding seasons, several territories still remain apparently quite deserted within this district. In three separate instances, it has been found that a breeding pair has used as an alternative nesting place a range of cliffs which formerly held a second pair, as if two territories may have become merged into one, so that peregrines seeking to occupy the second of the old territories may face competition. Similarly, some apparently vacant territories may actually be held by single non-breeders, which are seldom to be seen by human observers, but which effectively defend the territory against occupation by a breeding pair. This last effect probably occurs in some territories which are certainly known to have been held by single birds or non-breeding pairs for several years. Finally, even in 'normal' times, certain formerly regular territories were prone to unexplained periods of desertion, for no obvious reason. The only tenable explanation is that the nesting cliffs are only marginally suitable for peregrines, and prove attractive to only a small number of individuals.

It is quite probable that more than one—perhaps all— of these various inhibitory factors operate at present as a resistance to further recovery of the peregrine population. Nevertheless, the available evidence suggests that a heavy and enhanced mortality is the main factor inhibiting recovery in most depleted districts, and that this erodes the bulk of the annual population surplus which could restore numbers. This heavy mortality may operate locally against territory-holding adults or those which leave their nesting areas in winter, but it would seem to affect especially the young birds which move away from their birthplace to seek a place of their own.

The actual mortality rate for the whole population, based on the previous estimates, appears likely to approach 30% per annum, though this is a rather meaningless figure unless it is related to the state of the population as a whole. In a 'saturated' peregrine breeding population, an annual mortality of 30% or more might reflect stability through a lack of suitable habitat for expansion. In an 'unsaturated' population (as at present) a similar mortality has quite a different meaning, since the total population is only at about half the level which the habitat would allow. Other limiting factors must, therefore, be in operation. The overall figure of 30% also conceals the probable differential mortality between adult and 1st year birds; the higher the adult mortality, the greater the fragility of the remaining population.

There is no need to invoke any mortality factor other than that held responsible for the original population 'crash', namely contamination by persistent organochlorine residues. The recovery of peregrine population and its breeding success in northern inland districts is paralleled by reduction in residues of DDE and dieldrin in the eggs of birds from these districts, and indicates that a generalized reduction in use of some of the organochlorine insecticides during the years after 1962 has been beneficial to the species. There is still, however, a locally heavy use of these pesticides, and this increases with the proportion of

arable land. Heavy mortality among wild birds, notably the greylag goose, *Anser anser*; wood pigeon, *Columba palumbus*, and domestic pigeon, *C. livia*, in East Lothian during the winter of 1971 to 1972 was caused by the use of dieldrin seed dressings. Liver residues of dieldrin, in these and other species found dead, exceeded 10 parts/10^6 in many instances (G. Hamilton, personal communication). It is thus not surprising that peregrines, which take domestic pigeons as a principal prey species, should continue to be totally absent from their ancestral breeding haunts on the St Abbs coast. This is merely one example from an area where there happen to be obvious pointers to a continuing high mortality. There would seem to be strong probability that peregrines, which make their way into the more southerly and easterly parts of Britain, in general collect a body load of toxic chemical residues sufficient either to impair reproduction or to enhance the chances of premature death.

The prediction was made (Ratcliffe, 1965) that recovery of the British peregrine population would depend to a large extent on the scale of reduction in the use of persistent organochlorine pesticides. Whilst there has been improvement, the scale of use of such chemicals as DDT and dieldrin is still too heavy to allow more than partial recovery on a national scale. By contrast, the complete withdrawal of dieldrin sheep dips in 1966, because of human health hazards, was followed by a rapid and complete recovery in breeding success of western Scottish golden eagles, which had been feeding on contaminated sheep carrion and showed abnormally high breeding failure (including frequent egg breaking) between 1960 and 1966 (Lockie, Ratcliffe & Balharry, 1969). The lack of recovery in most coastal breeding populations of the peregrine, including remote districts of the western Highlands and Islands, Orkney and Shetland, suggests that, for these peregrines, the total exposure to toxic chemical residues in the coastal environment has not decreased. Although levels of DDE and dieldrin may have fallen, those of substances such as the PCBs have perhaps increased. It is noteworthy that peregrines breeding on or near the west coast of Scotland, where sea birds are likely to be an important part of the diet of many individuals, show appreciably higher levels of PCBs in their eggs than those which breed far inland. Attention has focused on the organochlorine pesticides, but other persistent compounds such as the PCBs have similar physiological effects; the possible rôle of other chemical pollutants (e.g. the heavy metals), to which peregrines are exposed through their food chain are not known. In six adult peregrines found dead or dying in 1971, liver residues of dieldrin ranged from 2·0 to 9·2 parts/10^6 (wet weight), DDE from 5·0 to 50·0 parts/10^6, mercury from 1·2 to 3·5 parts/10^6, whilst two of these birds from coastal breeding haunts had 60·0 and 200·0 parts/10^6 PCBs in the liver (Ratcliffe, 1972).

The other possible causes of the post-1965 decline in population and breeding success in the British peregrine have been discussed by Ratcliffe (1963, 1969); their contribution was judged to have been trivial or even negative. During the last decade, it is clear that rock-climbing has become increasingly inhibitory to the re-occupation of some cliffs, and in areas such as Northumberland, where the rocks are small, the peregrines attempting to hold a territory may be prevented from breeding. The illegal taking of young could become a serious factor, but egg-collecting has declined greatly for this species, and destruction of birds

by keepers is less than in former times. Casual disturbance at some coastal haunts may have made some of the smaller breeding cliffs unsuitable, but where cliffs are large and the nest-sites inaccessible, peregrines can endure the proximity of large numbers of people, as on the Sussex coast before the 'crash'. In short, there is no reason to believe that factors other than chemical pollutants are contributing significantly to the failure of peregrine recovery in those districts where numbers are not increasing.

General principles are emerging in pesticide–wildlife studies, but an impressive feature is the individual and idiosyncratic nature of response, both in regard to the species and the chemical involved. Moreover, the existence of geographical differences in peregrine–pollutant relationships within Britain implies that the field situation may also vary between different countries, and that the relative importance of adult mortality and reduced breeding success to population-decline may differ accordingly. In the United States south of Canada, it could well be that the once considerable but now almost vanished peregrine population was as a whole exposed to high levels of contamination by DDT and DDE, and that the total depression of reproductive performance was such that recruitment increasingly failed to balance mortality (Hickey & Roelle, 1969). Young (1969) has calculated that a decline of only 10% in productivity of young would cause a 6% reduction in a peregrine population over a 3-year period, assuming no change in mortality or other compensations; a 10% increase in nesting failure was estimated to give a similar order of population decrease. American ornithologists (e.g. White & Cade, 1971) are now extremely concerned about the reduced breeding success in Alaskan peregrines associated with marked eggshell thinning. Such a situation could be a sign of the steady collapse of the whole migratory peregrine population of the North American Arctic, which is much exposed to pollutant contamination outside the breeding season.

The chance existence in Britain of a relative refuge for the peregrine, in those inland districts of the Scottish Highlands where the species is sedentary and little exposed to pollutant contamination, has ensured that, in this country, a substantial part of the original population has maintained reasonably good breeding success. The present position, with significant recovery in both numbers and breeding success of the peregrine in those inland districts where exposure to persistent chemical pollutants has decreased, is a hopeful indication that these effects on population biology are reversible when the downward trends have not gone too far. The status of the coastal population, exposed to marine pollutants, is clearly more precarious and gives less ground for satisfaction.

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